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ARTICLE

Foraging under the risk of predation in desert grassland whiptail lizards (*Aspidoscelis uniparens*)

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Abstract The whiptail lizard *Aspidoscelis uniparens* searches for fossorial prey using a series of moves and pauses punctuated by bouts of digging. We examined the effect of predation risk on foraging *A. uniparens* in outdoor enclosures, observing their behavior in the presence and absence of the predatory lizard *Gambelia wislizenii*. Predator presence led to changes in activity patterns and foraging behavior. When predators were present, *A. uniparens* reduced both the proportion of time active and time moving, shifted activity periods, reduced their movement rate, and changed the duration of moves. There were no apparent changes in digging effort, but the likelihood of successfully digging for food decreased when a predator was present.

Keywords *Aspidoscelis* · Foraging · Lizard · Predation risk · Saltatory search

Introduction

Foragers alter their behavior to manage their own predation risk. Prey species can reduce the risk associated with foraging by reducing activity, enhancing vigilance, or altering habitat use and activity patterns (Lima and Dill 1990; Lima 1998). Reducing predation risk often involves a tradeoff with foraging efficiency (Sih 1980; Lima 1985; Lima et al. 1985). The extent of this tradeoff will depend on how a foraging strategy is modified in response to predators.

Saltatory search behavior, in which individuals alternately move and pause while foraging, is characteristic of a wide variety of animals (O'Brien et al. 1990). Prey are most often located during the pause phase of a saltatory search (O'Brien et al. 1986, 1990; Evans and O'Brien 1988;Avery 1993). Foragers are known to modify saltatory search behavior in response to changes in prey availability and detectability by altering pause and move characteristics (Evans and O'Brien 1988; O'Brien et al. 1989; Ehlinger 1989; Eifler and Eifler 1999). Saltatory search behavior is also likely to be influenced by a forager's vulnerability to predation.

In this study, we examined how a forager using saltatory searches responds to changes in predation risk. The lizard *A. uniparens* is a small diurnal predator living in arid environments of western North America. *A. uniparens* is unisexual (all individuals are female), and it does not exhibit territorial behavior; social interactions are very infrequent (Eifler and Eifler 1998). With its minimal social life, *A. uniparens* spends most of its time balancing two competing needs: finding food and avoiding predators. It feeds primarily on fossorial prey that it finds using a series of moves punctuated by bouts of digging (Eifler and Eifler 1998); foraging *A. uniparens* may be in motion 36% of the time and may only find food during a small proportion of digging episodes (approx. 20%; Eifler and Eifler 1998). The movement associated with its foraging has drawbacks: predators that may cue in to *A. uniparens* movement include snakes, other lizards, raptors, and roadrunners (*Geococcyx californianus*). *Aspidoscelis uniparens* modify elements of its search strategy in response to changes in food distribution (Eifler et al. unpublished data).

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Consequently, in this study, we also examined how components of its search strategy were modified when predation risk was experimentally increased.

Materials and methods

Our study site was located in the Chihuahuan desert grasslands of southeastern Arizona (Cochise County), approximately 5 km west of the border between Arizona and New Mexico. In our study area, *Aspidosceis uniparens* home ranges vary in size from 100 to 1575 m^2 (median = 770 m^2) and typically overlap those of 12 other individuals (Eifler and Eifler 1998). We constructed 6–15 × 15-m (225 m^2) experimental enclosures: three had predators introduced into them (=predator enclosures) and three remained predator-free (=control enclosures). Enclosure walls were 40 cm tall and constructed of 6-mm-thick opaque plastic sheeting supported by wooden stakes. The walls extended 15 cm below the surface to prevent lizards from digging out. Lizards were unable to see through or climb over the walls. Enclosure locations were selected to ensure similar plant cover and composition. The dominant plants were *Gutierrezia* spp., *Ephedra* spp., and *Prosopsis glandulosa*; vegetation cover in the enclosures ranged from 2.5 to 6.2%.

We populated each of the enclosures with six adult *A. uniparens* (Mean SVL = 69.8 mm; range = 62.0–75.0 mm) that were individually marked using unique color combinations of small plastic beads attached to a length of monofilament line inserted through the dorsal base of the tail. *Aspidoscelis uniparens* were placed in the enclosures within half a day of capture; we gave them 2 days to familiarize themselves with their enclosures prior to data collection. To each of the three predator enclosures, we also added two leopard lizards, *Gambelia wislizenii*, which are found in arid environments sympatric with *A. uniparens* (Stebbins 1985). Leopard lizards feed on whiptail lizards (Mitchell 1984), hunting them with a combination of ambush and stalking tactics (Tollestrup 1983; Pietruszka 1986). We introduced the *G. wislizenii* to predator enclosures 1 day after the *A. uniparens* had been introduced to the enclosures; *A. uniparens* were thus familiar with their enclosure prior to encountering a predator. Each *A. uniparens* was used in only one enclosure, but each leopard lizard was used in two predator enclosures: predation trials were conducted sequentially with three individual leopard lizards paired uniquely in each of the three predator enclosures. Trials in control enclosures were conducted concurrently with those in the predator enclosures. Both species of lizard were released near their capture location after their role in the study was completed.

We conducted focal observations from 6 to 21 July 2004 on clear, sunny days during *A. uniparens'* morning activity period (0700–1130 hours); observations were balanced between the two treatments within and between mornings to equalize conditions as much as possible. Observers stood outside the enclosure, approximately 1–2 m from the wall. The lizards did not respond to or seem to be affected by the observer's presence. We collected data on the lizards in each enclosure for 3 days, during which time we conducted focal observations on each *A. uniparens* one to three times. Each morning, active lizards were selected to observe based on the number of previous focals; priority was given to those farthest from our goal of three observations each. Focal observations lasted 15 min, although occasionally lizards disappeared from view (by going underground) before 15 min elapsed. Two observers occasionally conducted their respective focal observations on different lizards simultaneously at the same enclosure. For most of our observations, we recorded data on palmtop computers programmed to function as hand-held event recorders (HP 200LX; Hewlett Packard). Durations were recorded for the following behavioral states: moving, digging, and time under vegetation. We also recorded the frequency of movements and digging bouts. Digging bouts were regarded as successful if digging was immediately followed by prey consumption. Due to a shortage of palmtop computers, some observations were recorded with pencil-and-paper. These paper observations also lasted 15 min; to ensure data accuracy, we only recorded the frequency of digging bouts and whether digging was successful or not during paper observations.

In addition to focal observations, during the 3 days of data collection for each enclosure we conducted a census every 30 min during the *A. uniparens'* morning activity period. Census data were recorded by a single observer who spent 10 min walking along the outside perimeter of the enclosure, noting the identity of all visible lizards. We used census data to generate information on activity patterns.

For analyses, we summed the totals of multiple focal observations for individual *A. uniparens* to produce single summary values; we calculated behavioral rates by dividing the number of observed occurrences by the total time the animal was under observation. Likewise, we calculated the proportion of time devoted to specific activities by summing the durations of all occurrences and dividing the sum by the total time observed. For determining an individual's mean digging bout or movement duration, we averaged the durations for all observed instances. Data collected while a focal *A. uniparens* was within 30 cm of enclosure walls were excluded from analyses because proximity to the wall seems to be associated with altered movement patterns (personal observation). To test for an influence of predator presence, we performed ANOVAs to determine whether there were significant enclosure differences. Once we verified the absence of enclosure effects, we used *t*-tests to identify the effect of predator presence on *A. uniparens* behavior. The frequency distributions for movement duration, digging bout duration, digging success, and activity were compared by pooling all instances for lizards in the same treatment and conducting chi-square tests. We tested for shifts in whiptail activity relative to predator activity by computing the difference in predator and whiptail activity levels for both treatments during each census period and comparing the two treatments with a paired *t*-test. Statistical analyses were conducted using Minitab Release 13 (College Park, Pa.) with a significance level of $P \le 0.05$.

Results

We conducted focal observations on 32 *A. uniparens* (18 control; 14 predator). The predator-enclosures presented *A. uniparens* with a real risk of predation: *G. wislizenii* was observed chasing *A. uniparens*, and twice we observed *G. wislizenii* successfully capturing and consuming *A. uniparens* in our predator enclosures. Lizards that became prey were not replaced. Two additional lizards introduced to the predator enclosures, although seen during censuses, were never detected when observations were being conducted. When we tested for enclosure effects on behavior, in only one instance was there significant variation among enclosures within treatment (Table 1): the amount of time spent in vegetation varied among control enclosures ($F_{2,15} = 7.57$, $P = 0.005$). For time spent in vegetation, enclosures, not individual lizards, were used for subsequent analyses.

The presence of predators resulted in fewer sightings of *A. uniparens* during censuses (= shortened activity periods; $t_{30} = 7.89$, $P < 0.0001$; Table 2). Lizards in the predator enclosures and in control enclosures did not differ in terms of the distribution of their active times ($\chi^2_8 = 15.1$, $P = 0.056$; Fig. 1), but they did differ significantly in terms of the pattern of their morning activity relative to predator activity ($t_9 = 4.09$, $P = 0.003$; Fig. 1). Whiptails in the predator enclosures shifted their activity patterns away from periods of peak predator activity. In predator enclosures, whiptails were most active before the predators became active (0800 hours); they then remained less active than the predators until the end of their morning activity period (1100 hours; Fig. 1).

Lizards in the predator enclosures spent less time moving ($t_{23} = 2.69$, $P = 0.013$) and moved less often (= movement rate) than lizards in control enclosures ($t_{25} = 3.36$, $P = 0.003$; Table 2). Although the mean movement duration did not differ relative to predator presence ($t_{26} = 1.06$, $P = 0.298$), the distribution of move durations did differ among treatments ($\chi^2_5 = 34.4$, $P < 0.001$). Lizards in predator enclosures made proportionately fewer very short moves (≤2 s) and more moves of longer duration than control enclosure lizards (Fig. 2).

The proportion of time lizards spent digging did not differ between the treatments ($t_{25} = 0.22$, $P = 0.825$), nor did predator presence influence digging rates ($t_{25} = 0.16$, $P = 0.876$; Table 2). Similarly, neither mean digging bout duration nor the distribution of digging bout durations differed between treatments (mean digging bout duration: $t_{29} = 0.50$, $P = 0.619$; distribution of digging bout durations: $\chi^2_5 = 3.89$, $P = 0.56$). However, digging by whiptails in control enclosures was more likely to result in obtaining food than digging by whiptails in predator enclosures ($\chi^2_1 = 11.0$, $P = 0.001$). Animals in control enclosures

Table 1 Results of ANOVA tests examining whether whiptail behavior was influenced by their enclosure

Behavior	Control		Predator	
	F	*P*	*F*	*P*
Time in vegetation (%)	7.57	0.005	0.34	0.716
Activity period (census sightings/day)	0.2	0.819	1.39	0.287
Time moving (%)	2.99	0.081	0.55	0.592
Movement rate (moves/min)	0.93	0.417	0.77	0.488
Movement duration (s)	0.24	0.787	0.12	0.892
Time digging (%)	0.85	0.448	0.33	0.729
Digging rate (digs/min)	1.57	0.240	0.97	0.409
Dig duration (s)	1.76	0.206	0.01	0.991

Table 2 Comparison of behavioral data for *Aspidoscelis uniparens* in the absence and presence of predators (*Gambelia wislizenii*)

Measurement	Control enclosures	Predator enclosures
Time in vegetation (%)	36.8 (4.3)	53.6 (6.9)
Activity period (census sightings/day)	5.8 (0.3)	2.7 (0.2)*
Time moving (%)	26.8 (1.8)	18.1 (2.7)*
Movement rate (moves/min)	8.2 (0.6)	4.1 (0.9)*
Movement duration (s)	2.2 (0.2)	2.5 (0.3)
Time digging (%)	1.2 (0.2)	1.1 (0.3)
Digging rate (digs/min)	0.5 (0.08)	0.5 (0.11)
Dig duration (s)	1.6 (0.3)	1.4 (0.2)

Values are presented as means (standard error)

* Significant differences ($P \le 0.05$) between whiptails in control and predator enclosures. Test statistics are provided in the text

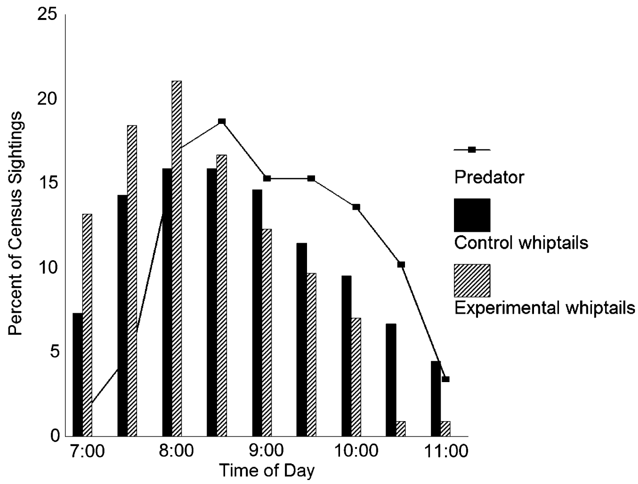

Fig. 1 Activity patterns for *Aspidoscelis uniparens* in the absence (control whiptails) and presence (experimental whiptails) of the predatory lizard *Gambelia wislizenii*. The *solid line* represents the activity of the predators during the same time period

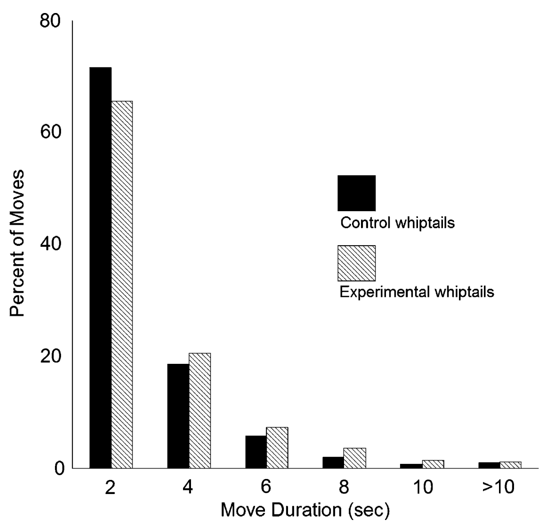

Fig. 2 Movement durations for *A. uniparens* in the absence and presence of the predatory lizard *G. wislizenii*. The frequency distributions were assembled using 4306 predator-absent and 1784 predator-present movements timed during focal animal observations

experienced 43.8% digging success, while experimental animals found food during only 31.2% of digging bouts.

Discussion

Our study demonstrates that *A. uniparens* responds to enhanced predation risk by altering aspects of both their activity and their foraging strategies. Most of these changes have the potential to reduce predation risk: shortening and shifting activity periods can decrease the likelihood of encountering predators; reducing the proportion of time spent moving and the rate of movement may reduce the conspicuousness of foraging *A. uniparens* and allow more time and attention to be devoted to vigilance. These results are consistent with other studies demonstrating that prey can reduce predation risk by adjusting their activity (Sih 1992; Downes and Shine 2001; Downes 2002). However, every observed reduction in activity may lead to reductions in prey encounters, which may account for why other components of *A. uniparens* search behavior were not modified as would be expected of animals lowering their predation risk. In particular, the digging behavior and pattern of movement durations of *A. uniparens* in the presence of predators may be best understood within the context of foraging tradeoffs.

Digging is a conspicuous activity, at least to humans, and one likely to divert the attention of a digging *A. uniparens* away from predator detection. However, predator presence was not associated with any changes in digging frequency or in the amount of time devoted to digging. It may be that digging does not increase *A. uniparens'* conspicuousness or vulnerability to *G. wislizenii.* Alternatively, digging may be a component of their foraging behavior that cannot be modulated without a prohibitive reduction in foraging success. *Aspidoscelis uniparens* in predator enclosures were less likely to find food during a digging bout than those in control enclosures; changes in their allocation of attention to foraging and vigilance may have contributed to this reduction in digging success. Less attention to a difficult task such as foraging can result in more effective vigilance and lower predation risk (Dukas and Clark 1995; Brown 1999; Kotler et al. 2002), whereas foragers devoting more attention to predator detection make greater and more frequent mistakes in foraging-related activities (Dall et al. 2001; Kotler et al. 2004). Furthermore, increases in predation risk can lead to reduced effectiveness in terms of prey detection and recognition (Metcalfe et al. 1987a, b). In our study system, less attentive foragers may be less adept at selecting digging sites, with the result that digging performance, but not digging effort is influenced by predators. Further attention to the relationship between digging effort and factors influencing digging performance is merited.

The second aspect of *A. uniparens'* foraging behavior shaped by tradeoffs centering on reducing predation risk is their pattern of movement durations. *A. uniparens* altered the distribution of their movement durations by reducing their proportion of very short moves. Saltatory searchers looking for hard to detect prey are expected to move short distances between pauses (Andersson 1981; Getty and Pulliam 1991; Anderson et al. 1997). A reduction in the frequency of short moves under predator pressure may occur if short moves are particularly conspicuous to predators or if a forager is less likely to make them when distracted. Further investigation is needed to determine the criteria dictating the extent to which move durations and other aspects of foraging behavior are modified to maintain a balance between predation risk and finding enough food. The response of *A. uniparens* to the presence of a predator demonstrates flexibility in how the elements of their foraging behavior are assembled, but underscores the extent to which reducing predation risk is part of a tradeoff with foraging efficiency.

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References

Anderson JP, Stephens DW, Dunbar SR (1997) Saltatory search: a theoretical analysis. Behav Ecol 8:307–317

Andersson M (1981) On optimal predator search. Theor Popul Biol 19:58–86

Avery RA (1993) Experimental analysis of lizard pause-travel movement: pauses increase probability of prey capture. Amphibia-Reptilia 14:423–427

Brown JS (1999) Vigilance, patch use and habitat selection: foraging under predation risk. Evol Ecol Res 1:49–71

Dall SRX, Kotler BP, Bouskila A (2001) Attention, 'apprehension' and gerbils searching in patches. Ann Zool Fennic 38:15–23

Downes SJ (2002) Does responsiveness to predator scents affect lizard survivorship? Behav Ecol Sociobiol 52:38–42

Downes SJ, Shine R (2001) Why does tail loss increase a lizard's later vulnerability to predators? Ecology 82:1293–1303

Dukas R, Clark CW (1995) Sustained vigilance and animal performance. Anim Behav 49:1259–1267

Ehlinger TJ (1989) Learning and individual variation in bluegill foraging: habitat-specific techniques. Anim Behav 38:643–658

Eifler DA, Eifler MA (1998) Foraging behavior and spacing patterns of the lizard *Cnemidophorus uniparens*. J Herpetol 32:24–33

Eifler DA, Eifler MA (1999) The influence of prey distribution on the foraging strategy of the lizard *Oligosoma grande* (Reptilia: Scincidae). Behav Ecol Sociobiol 45:397–402

Evans BI, O'Brien WJ (1988) A reevaluation of the search cycle of planktivorus arctic grayling, *Thymallus arcticus*. Can J Fish Aquat Sci 45:187–192

Getty T, Pulliam HR (1991) Random prey detection with pause-travel search. Am Nat 138:1459–1477

Kotler BP, Brown JS, Dall SRX, Gresser S, Ganey D, Bouskila A (2002) Foraging games between gerbils and their predators: temporal dynamics of resource depletion and apprehension in gerbils. Evol Ecol Res 4:495–518

Kotler BP, Brown JS, Bouskila A (2004) Apprehension and time allocation in gerbils: the effects of predatory risk and energetic state. Ecology 85:917–922

Lima SL (1985) Maximizing feeding efficiency and minimizing time exposed to predators: a trade-off in the black-capped chickadee. Oecologia 66:60–67

Lima SL (1998) Stress and decision making under risk of predation: recent developments from behavioral, reproductive, and ecological perspectives. Adv Study Behav 27:215–290

Lima SL, Dill LM (1990) Behavioral decisions made under the risk of predation: a review and prospectus. Can J Zool 68:619–640

Lima SL, Valone TJ, Caraco T (1985) Foraging–efficiency–predation–risk trade-off in the grey squirrel. Anim Behav 33:155–165

Metcalfe NB, Huntingford FA, Thorpe JE (1987a) The influence of predation risk on the feeding motivation and foraging strategy of juvenile Atlantic salmon. Anim Behav 35:901–911

Metcalfe NB, Huntingford FA, Thorpe JE (1987b) Predation risk impairs diet selection in juvenile salmon. Anim Behav 35:931–933

Mitchell JC (1984) Observations on the ecology and reproduction of the leopard lizard, *Gambelia wislizenii* (Iguanidae), in southeastern Arizona. Southwestern Nat 29:509–511

O'Brien WJ, Evans BI, Howick GL (1986) A new view of the predation cycle of a planktivorus fish, white crappie (*Pomoxis annularis*). Can J Fish Aquat Sci 43:1894–1899

O'Brien WJ, Evans BI, Browman HI (1989) Flexible search tactics and efficient foraging in saltatory searching animals. Oecologia 80:100–110

O'Brien WJ, Browman HI, Evans BI (1990) Search strategies of foraging animals. Am Sci 78:152–160

Pietruszka RD (1986) Search tactics of desert lizards: how polarized are they? Anim Behav 34:1742–1758

Sih A (1980) Optimal behavior: can foragers balance two conflicting demands? Science 210:1041–1043

Sih A (1992) Prey uncertainty and the balancing of antipredator and feeding needs. Am Nat 139:1052–1069

Stebbins RC (1985) A field guide to western reptiles and amphibians. Houghton Mifflin Company, Boston

Tollestrup K (1983) The social behavior of two species of closely related leopard lizards, *Gambelia silus* and *Gambelia wislizenii*. Z Tierpsychol 62:307–320